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THE UNIVERSITY OF ALBERTA
AN ECOLOGICAL STUDY OF RED-NECKED GREBES
ON ASTOTIN LAKE, ALBERTA

by



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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled An Ecological Study of Red-necked Grebes on Astotin Lake, Alberta, submitted by Cora Louise Kevan in partial fulfilment of the requirements for the degree of Master of Science.

Abstract

Red-necked Grebes were studied on Astotin Lake in Elk Island National Park, Alberta during the spring and summers of 1968 and 1969. This lake has a large population of grebes nesting at different densities and in different habitats. In 1969, 212 grebe nests were examined.

The birds arrived on Astotin Lake in late April, some apparently already paired. The peak of nesting did not occur until the last half of May when most clutches were initiated. Most hatching occurred between June 16 and June 25, 1969. The average clutch size was 5.2 eggs; the average brood size was 1.8. Known egg and chick losses were highest in areas of high nesting density. Some evidence of renesting was found.

The success of nesting Red-necked Grebes seemed dependent on three basic requirements of the nest site: 1) easy swimming access to the site, 2) nest material close to the site, 3) protection from wave action. These characteristics were met in sedge marshes where nests were most numerous.

Territories of Red-necked Grebes were found to differ in size and type. Pairs nesting close together had more agonistic interactions than those farther apart. The location of the nest in the marsh also affected the number of agonistic interactions. Territorial behaviour of established pairs delayed or prevented the nesting of other

pairs.

The reaction of pairs to the experimental shifting of nest sites varied. For three of the five pairs the territory shifted with the nest site. Development of a dominance hierarchy was also noted. The subordinate pairs deserted before they had hatched all of their eggs.

Nest site availability was thought to be the prime factor controlling the spacing of nests on the lake. Pairs were attracted to areas with suitable nest sites. They then usurped parts of territories of previously established pairs. Agonistic interactions between pairs may account for some egg and chick losses in areas of high nesting density. In such areas dominance hierarchy systems may be established which lead to desertion of nests by subordinate pairs before hatching is complete.

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1. Introduction

The way birds use their habitat affects their density and may have a role in regulating their numbers (Wynne-Edwards, 1962; Lack, 1966). Habitat utilization during the breeding season has many facets, including habitat preference, habitat availability, territoriality and agonistic behaviour of the birds. These factors have been little studied in the Podicipedidae.

Six of the twenty known species of Podicipedidae occur in North America. Of the North American species two are usually colonial, the Eared Grebe (*Podiceps caspicus*), and the Western Grebe (*Aechmophorus occidentalis*); three are usually solitary, the Horned Grebe (*Podiceps auritus*), the Pied-billed Grebe (*Podilymbus podiceps*), and the Least Grebe (*Podiceps dominicus*); the remaining species, the Red-necked Grebe (*Podiceps grisegena*) nests either solitarily or in loose colonies (Palmer, 1962).

Reports of the Red-necked Grebe nesting in colonies are vague. Bent (1919:10) found "what might be called a colony, seven nests..." and refers to Currier (1904) who found a colony of between six and ten pairs. Unfortunately neither of these two authors give distances between nests in these "colonies". Silloway (1902) found seven nests, all separated by at least 100 meters in a marsh in Montana. In his review of Silloway's

paper, Bent (1919) referred to this as a colony. Munro (1941) found these grebes nesting on Swan Lake in the Okanagan Valley of British Columbia. They had territories which usually included 75 to 125 yards of shoreline; but some nests were as little as 10 yards apart. Even so, Munro felt that they were not colonial. The use of the terms "colonial" and "solitary" in reference to Red-necked Grebes has so far indicated only that in some areas the birds are more numerous than in others. Whether this results from different availabilities of nest habitat from place to place or from variation in the nesting behaviour of the birds is unclear.

Territoriality in grebes is different in each species studied. The territories of Pied-billed Grebes usually include an area with a radius of 150 feet around the nest (Glover, 1953). Hartley (1933) found that different pairs of Little Grebes (*Podiceps ruficollis*) were similarly aggressive and held territories of about equal size. These territories were held until the young were fully grown. He found no colonies.

The Great Crested Grebe (*Podiceps cristatus*) is reported to nest both solitarily and colonially. In a five year study of these birds, Venables and Lack (1934, 1936) found great variation in the aggressiveness of individuals and the sizes of their territories. They concluded that territories were not of primary significance in pair formation, and did not usually include the feeding

grounds.

Little is known about the nesting requirements of grebes. Gotzman (1965) investigated the environmental preferences of Great Crested, Red-necked, Eared, and Little Grebes nesting in Poland. He found that the grebes nested in emergent vegetation of "medium density" (see p. 43) and that the different species segregate according to water depth and distance from the open flood (water free of emergent vegetation). Glover's (1953) study of the Pied-billed Grebe shows that those nests closer to shore are more subject to predation and stranding on dry land when the water level in the marsh drops. He found no correlation between vegetation density at the nest site and nesting success.

I undertook this study to investigate the factors affecting the nesting dispersion of the Red-necked Grebe at Astotin Lake in Elk Island National Park, Alberta. Information was gathered on the general biology of the bird on the lake. The environmental characteristics of the nest site were then examined. I then attempted to determine the roles that the availability of nest sites and territoriality play in the nesting of the Red-necked Grebe on Astotin Lake.

2. The Study Area

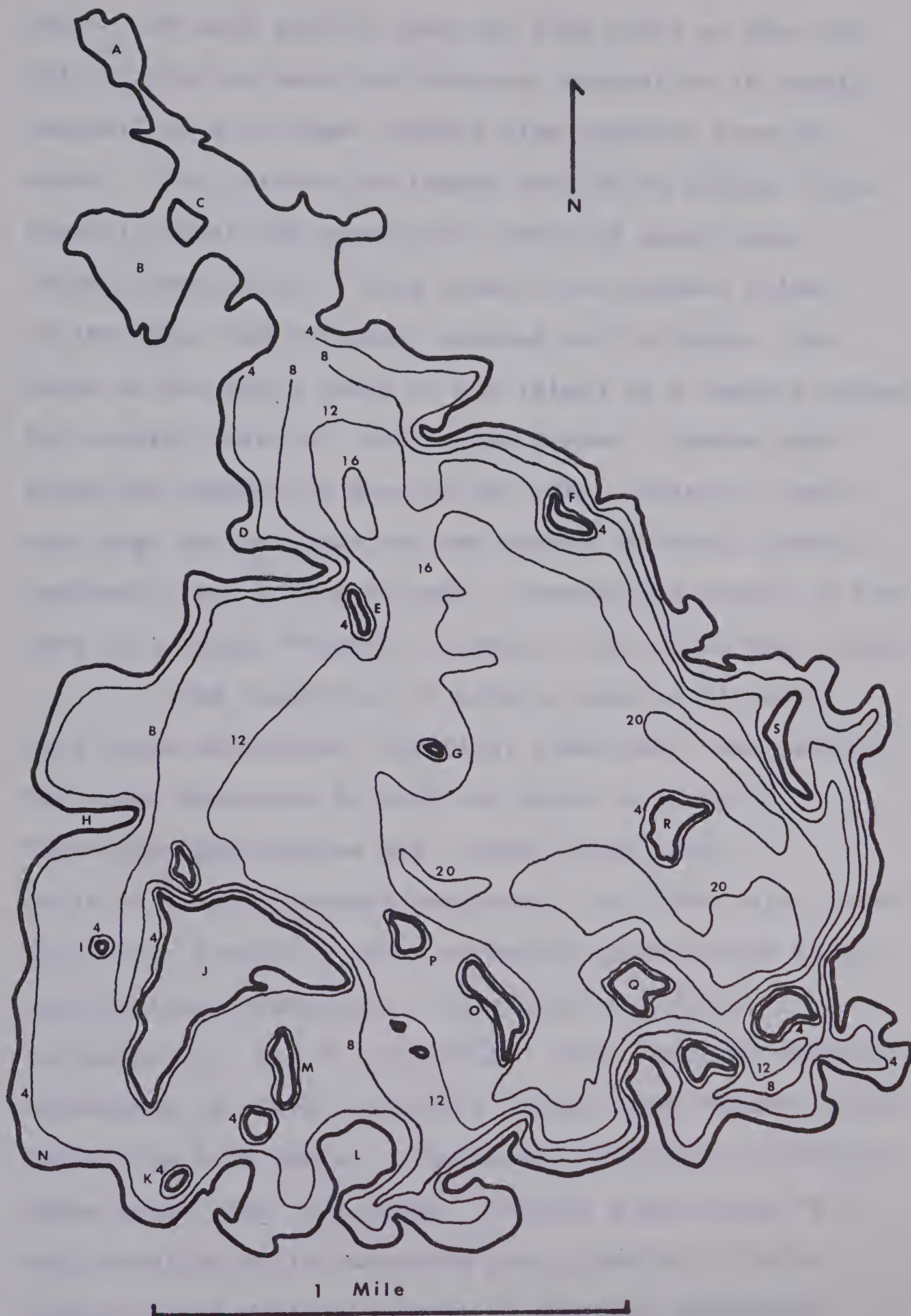
My study area was Astotin Lake in Elk Island National Park, located twenty-three miles east of Edmonton, Alberta. The lake has a longitude of 112°51'West and a latitude of 53°41'North. A large population of Red-necked Grebes nest on the lake in various habitats and at different densities. The park encompasses 72 square miles of aspen parkland in the Beaver Hills area. These hills, also known as the Cooking Lake moraine, were formed after the Wisconsin glaciation. The topography is characterized by typical moraine features of knobs and numerous kettles.

Astotin Lake, a kettle lake, is the largest of several lakes within the park boundary. The lake has an area of 5.616 km², and an average depth of 3.04 meters (Fig. 1). Because of its shallowness, and high productivity, the lake is very eutrophic (Lin, 1968). The lake has a sinuous shoreline some 19.5 km. long, providing numerous protected bays. These bays support rank growths of emergent vegetation such as sedges (*Carex* spp.), cattail (*Typha latifolia*), bulrushes (*Scirpus* spp.) and others. It is in these bays that nesting Red-necked Grebes are most numerous.

There are seventeen islands on the lake, providing more shoreline and emergent vegetation. The islands

Figure 1. A contour map of Astotin Lake, Elk Island National Park, Alberta, ($112^{\circ} 51' \text{ W.}, 53^{\circ} 41' \text{ N}$). The water depth is shown at 4 foot contour intervals. Islands and study areas are indicated by letters. (Redrawn from Lin, 1968).

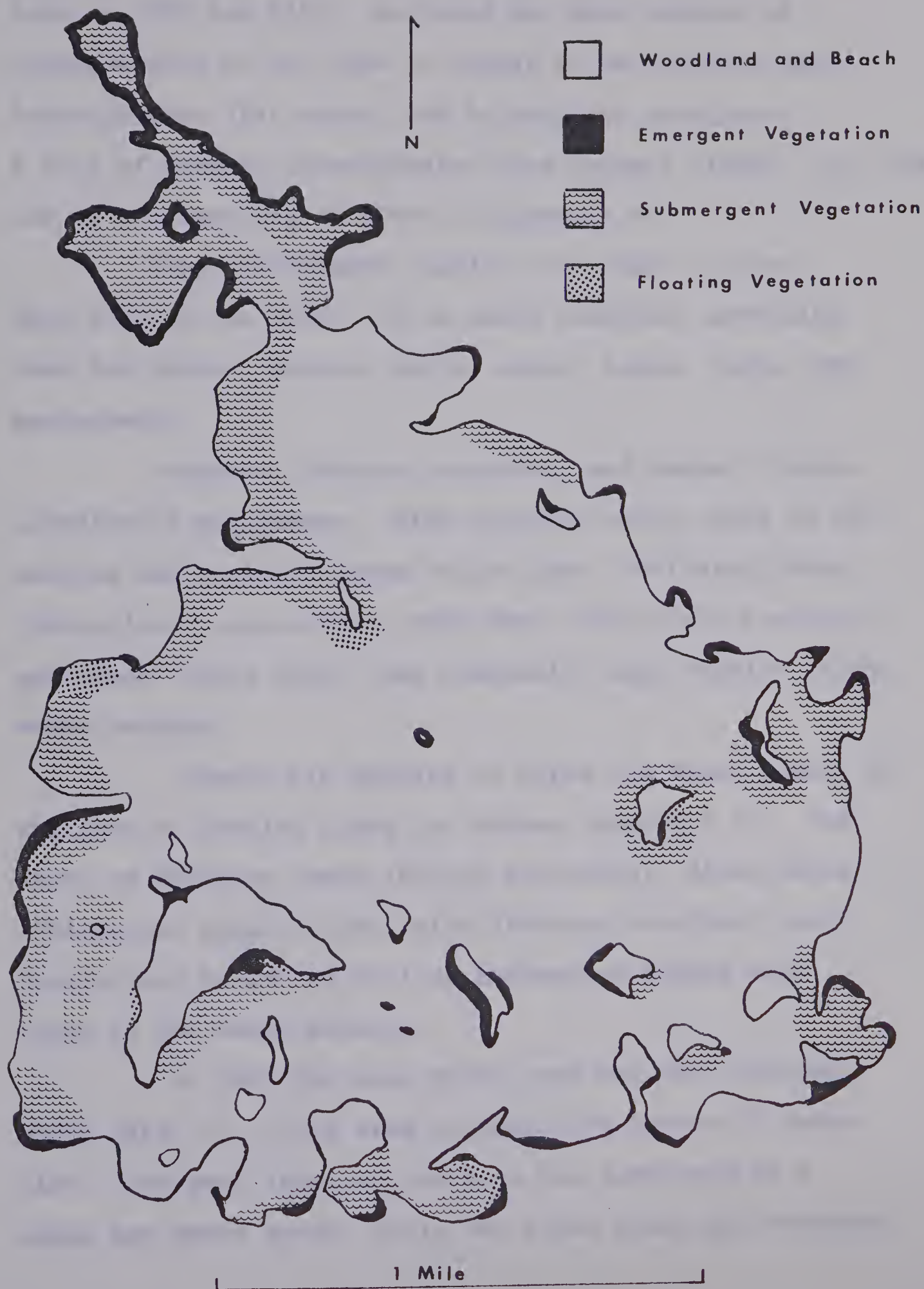
- A Creek Cove
- B Northwest Cove
- C Cove Island
- D Martin Bay
- E Point Island
- F North Island
- G Reed Island
- H Long Island Point
- I Willow Clump
- J Long Island
- K Heron Island
- L Elk Island
- M Line Island
- N Southwest Shore Study Area
- O Crane Island
- P Lamont Island
- Q Archer Island
- R High Island
- S Raspberry Island



shelve off more quickly than the lake shore so that the belt of shallow water and emergent vegetation is usually narrow. Most of these islands rise abruptly from the water. The islands are topped with white spruce (*Picea glauca*) forest and occasional clones of paper birch (*Betula papyrifera*). Long Island, the largest island on the lake, has two sedge marshes on its shore. The marsh on the south shore of the island is a nesting ground for several pairs of Red-necked Grebes. Rushes grow along the borders of some of the other islands. There are large bulrush beds off the shores of Crane, Lamont, Raspberry, and Archer Islands. Towards the center of the lake is a large *Phragmites communis* bed called Reed Island.

The vegetation of Astotin Lake is divisible into three categories: floating, submergent, and emergent. The areas dominated by each are shown in Figure 2. Three floating species are found: *Lemna minor*, *L. trisulca*, and *Polygonum amphibium*. Lin (1968) also found *Sagittaria cuneata*. Four submerged species were found: *Myriophyllum exalbescens*, *Potamogeton pusillus*, *P. richardsonii*, and *P. vaginatus*. The dominant emergent vegetation is *Carex aquatilis* which forms marshes along 29% of the lake shore. The grass, *Scolochloa festucacea* often grows with this sedge. Cattail grows along 7% of the shoreline while bulrushes grow along 6%. The location of the various species of emergent vegetation

Figure 2. A map of Astotin Lake showing the location of emergent, submergent, and floating vegetation on the lake.



along the lake shore is shown in Figure 3.

Lin (1968) made limnological studies of the lake in 1966 and 1967. He found the main species of phytoplankton in the lake in summer to be *Anabaena* spp., *Aphanizomenon flos-aquae*, and *Microcystis aeruginosa*. A list of aquatic invertebrates from Nursall (1968), Lin (1968), and my own sampling is given in Appendix A.

The stickleback (*Culaea inconstans*) is the only fish in the lake. It is quite numerous, providing food for grebes, herons, gulls, coots, terns, loons, and mergansers.

Muskrat (*Ondatra zibethica*) and beaver (*Castor canadensis*) are common. Mink (*Mustela vison*) hunt in the marshes and on the islands of the lake. Whitetail deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*) and moose (*Alces alces*) are frequently seen feeding in the sedge marshes.

Twenty-six species of birds are found either on the lake or nesting along its shores (Appendix B). The nests of American Coots (*Fulica americana*), Black Terns (*Chlidonias niger*), Sora Rails (*Porzana carolina*), and Pied-billed Grebes as well as Red-necked Grebes were found in the sedge marshes.

In 1969 the main study area was the southwest shore (Fig. 1). This area included 274 meters of shoreline. The west shore of the area was dominated by a sedge and grass marsh, while the south shore was bordered

Figure 3. A map of Astotin Lake showing the shoreline habitats, including the location of various species of emergent vegetation. The locations of blinds are also shown.



Woodland



Sedge and Grass



Cattail



Willow



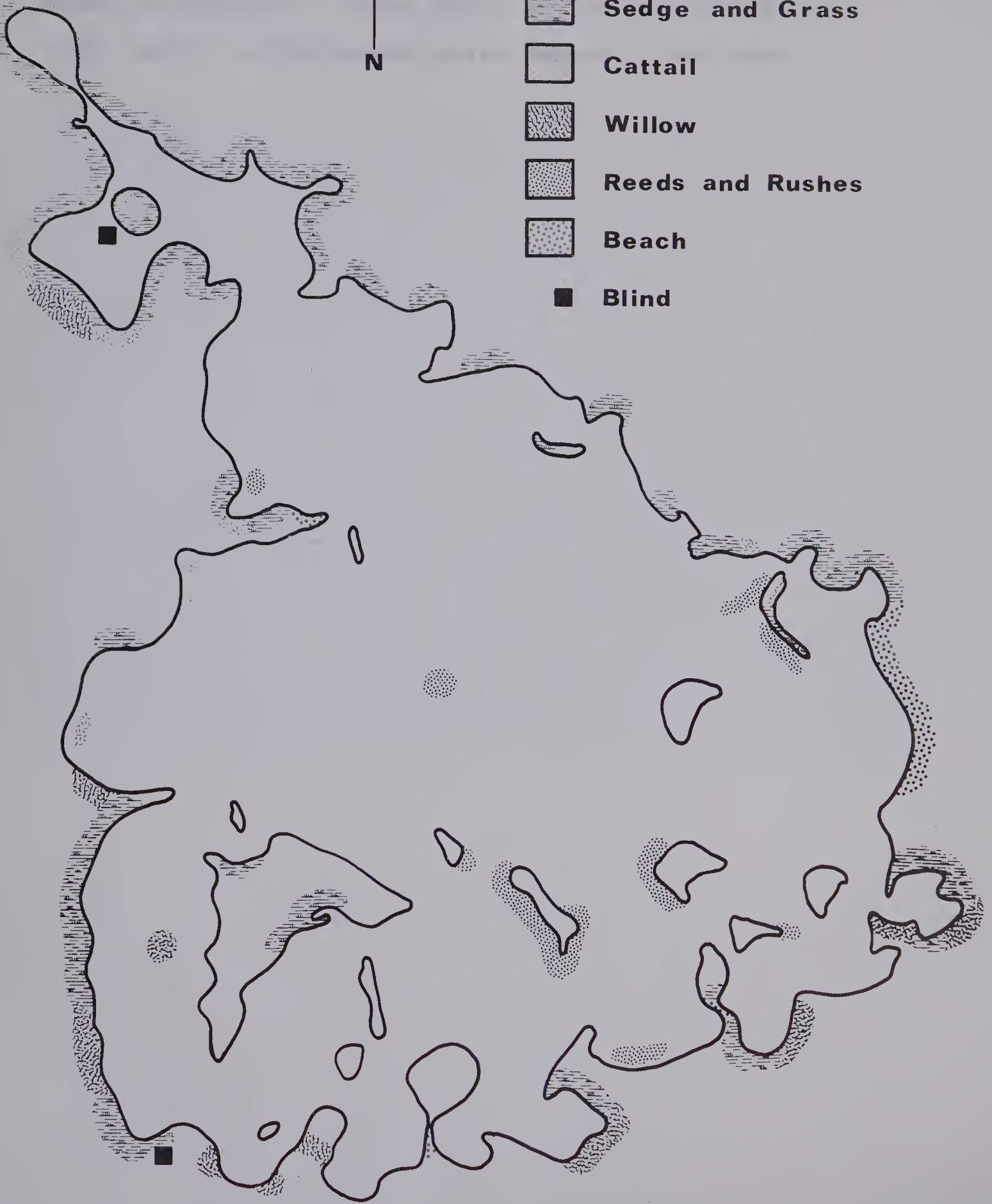
Reeds and Rushes



Beach



Blind



1 Mile



by woodland and willows. A photograph of the area is shown in Figure 4. Seven pairs nested in the area in 1968, while in 1969 eight pairs nested in the area.

Figure 4. The southwest shore study area on
Astotin Lake in early May 1969.



3. Materials and Methods.

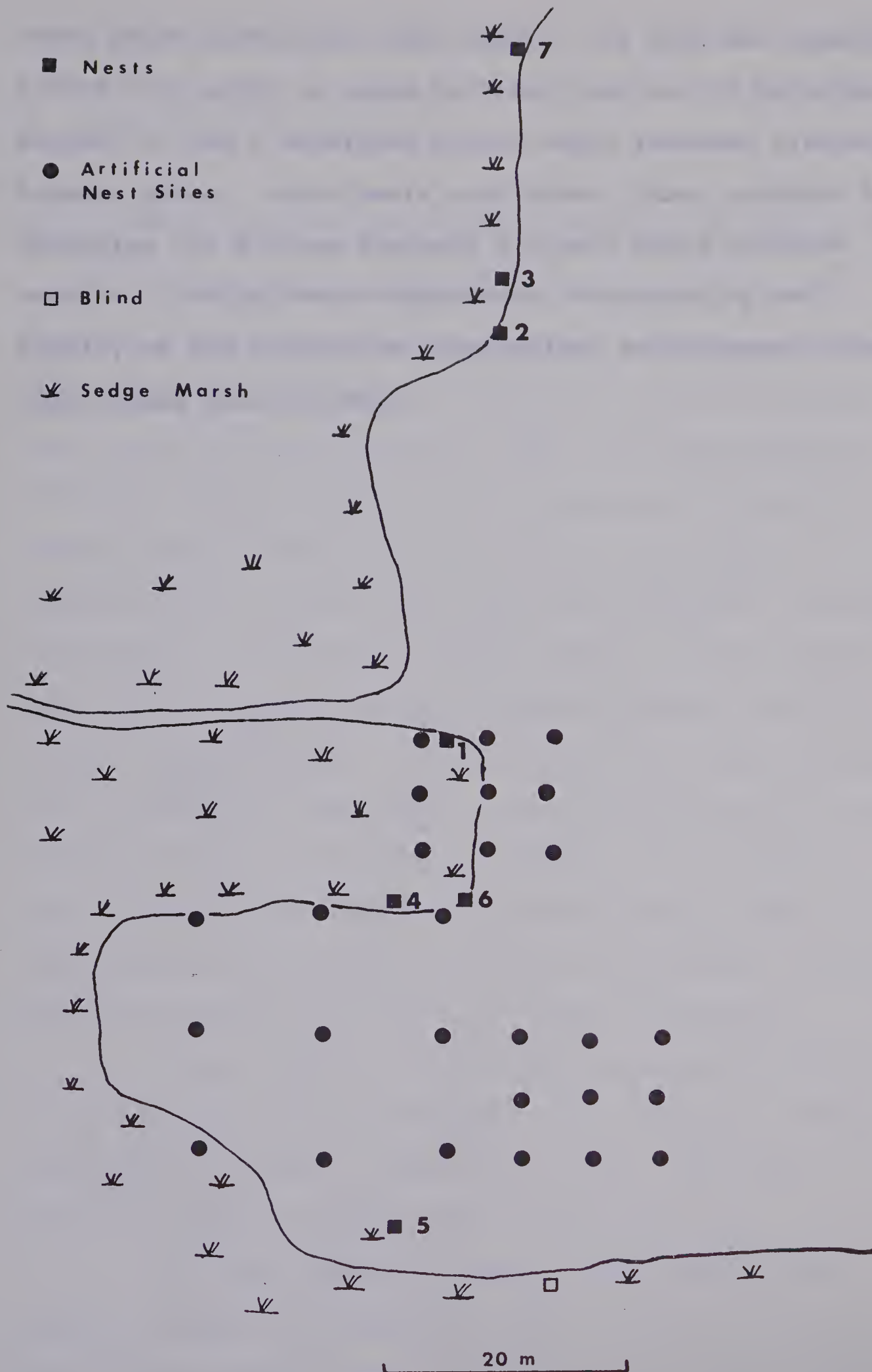
This study was conducted from May through August in 1968 and 1969. I watched the grebes through binoculars or a telescope openly from the shore or from a boat, or from either of two blinds, one on the shore and one floating (Fig. 3). Nests were investigated by boat or by wading out to them.

The timing of the major events of the reproductive cycle were recorded. Clutch size, hatching success, and brood size were investigated in different regions of the lake. Characteristics of the nest site were examined including water depth, species and growth form of surrounding vegetation, and the height and circumference of the hummocks located at each site. To test whether the grebes were using areas of marsh of a particular vegetation density, distances from nests and random points to the closest sedge hummocks not touching the nests or random points were measured using the quarter method (Smith, 1966:617-618). The circumferences of the hummocks were also measured and the basal area was calculated. The results were then analyzed with t tests (Appendix D). The distances of each nest to its closest neighbour, to shore, and to open water were measured.

In sedge marshes, thickly growing vegetation was considered to be the shore even if the ground was not dry. Water free of emergent vegetation was considered open water. Because in 1968 I found many nests resting on supporting objects I decided to establish artificial nest sites in the southwest shore to see if I could increase the density of nesting birds there. Three grids of nine artificial nest sites were established. In the first grid the sites were located 10 meters apart. In the second and third grids the sites were 5 meters apart. These sites consisted of chicken wire cylinders 25 cm in diameter anchored to the substrate with stakes and stayed with bricks. The cylinders were then filled with vegetation and mud from the lake bottom. The mean water depth at these sites was 39.5 cm. Ten of these sites were established by sedge hummocks; the others were established in open water. I felt that nesting material was available near each nest site. The location of the artificial nesting sites and the nest sites of the pairs that established in the study area are shown in Figure 5.

Throughout May and June of 1969 pairs in the southwest shore area were observed. The birds were not marked, but the pairs stayed in the same general areas from day to day, and so were thought to be the same pairs. From observations of agonistic interactions between

Figure 5. A map of the southwest shore study area showing the location of the artificial nest sites and the location of the nests of pairs that established in the area.



these pairs, territories were mapped. In June the vegetation around five nests in close proximity was cut to determine whether it had a shielding effect which lessened interactions between pairs. Later nests were moved closer together to determine the minimum distance one pair would tolerate another. During these experiments, the quantity and quality of the aggressive interactions and changes in the territories were recorded.

4. Results and Discussion

4.1 Wintering and Breeding Ranges; Arrival on Astotin Lake.

There are two subspecies of Red-necked Grebe.

Podiceps grisegena grisegena is found in Europe and western Asia. *Podiceps grisegena holbollii* is found in eastern Asia and North America (Wobus, 1964). In North America, Red-necked Grebes winter along the Atlantic and Pacific coasts ranging from Nova Scotia to the east coast of Florida in the Atlantic, and from the Aleutians to southern California in the Pacific (Palmer, 1962). In the spring they return to their breeding grounds in Canada and the northern United States. It is thought that birds wintering along the Pacific coast nest in the western portion of the breeding range, but banding recoveries are too few to give any definite information on this (Palmer, 1962). A map showing the breeding and wintering grounds, and the migration routes of the birds is shown in Figure 6.

Munro (1941:2) stated that first arrival dates in the Okanagan, British Columbia were irregular, ranging from March 1 in 1917 to March 21 in 1919. The main migration occurred between April 20 and April 30.

In 1969 Red-necked Grebes were sighted near Calgary on April 26 (Wershler, 1969). The first birds were seen on Astotin Lake and ponds in Elk Island National

Figure 6. A map showing the breeding and wintering ranges, the migration route, and areas of postbreeding dispersal of the Red-necked Grebe. It also shows the location of Elk Island National Park. (Redrawn from Palmer, 1962).



||| Breeding

~ Winter

▦ Migration

- - Postbreeding
Dispersal

▲ Elk Island
National Park

Park on April 29, 1969. Most of these birds were in open water performing courtship ceremonies, while others were in the marshes already building nest platforms and copulating.

4.2 Courtship.

Displays and ceremonies resulting in formation and strengthening of a bond between members of a pair are considered courtship (Storer, 1969). Storer (1969) describes the complex courtship ceremonies for the genus *Podiceps* and illustrates those of the Horned Grebe. The Red-necked Grebe performs three principal ceremonies: "Discovery", "Head Shaking" and "Weed". They are similar to those of the Horned Grebe (Storer, 1969). Storer considers that the "Discovery" ceremony is the prime factor in forming and strengthening the pair bond, while "Weed" ceremonies were probably derived from nest building activities. "Head Shaking" ceremonies become more frequent after pair formation and are used less frequently as nesting proceeds.

The platform behaviour (precopulatory and copulatory) of all grebe species is similar (Storer, 1963). There are three soliciting displays: "Inviting", "Rearing", and "Wing Quivering". Of the three, "Inviting" is performed most frequently, "Wing Quivering" the least. These displays are usually performed on platforms, though

"Inviting" can occur in the water.

Copulation usually occurs on platforms built by the pair (Storer, 1969; Wobus, 1964: pers. obs.). Johnstone (1953) reported a copulation on a partially submerged pine, and I observed copulation on artificial nest sites. Glover (1953) and Kilham (1954) reported that Pied-billed Grebes copulate in open water, but this was rejected by McAllister and Storer (1963) because the Podicipedidae do not have intromittent organs.

At Astotin Lake most pair formation seemed to take place on open water near nesting areas. Some birds may have arrived already paired as birds were seen building nests and copulating on the arrival date in 1969.

The establishment of territories by male Great Crested Grebes, and the subsequent attraction of females was observed by Venables and Lack (1936). This was not observed on Astotin Lake. Most grebes which investigated the southwest shore came in pairs. They lingered in the open water performing "Head Shaking" and "Weed" ceremonies, and "Inviting" in the open water. When they approached the shore they were threatened by established pairs.

4.3 Nest building.

Nest building was first observed on April 29, 1969, peaked during the last two weeks in May, and was last seen in late July in both years. Nests were

constructed by both sexes and were continually added to throughout the nesting period.

The birds frequently built several flimsy platforms before constructing the definitive nest. In the southwest shore study area five of the seven pairs built one platform before building a definitive nest. Two pairs built two platforms. Pairs 4, 5, and 6 (Fig. 5) investigated the artificial nest sites and also constructed their own nest platforms. The platforms and artificial nest sites were used for soliciting and copulation. The pairs were not consistent in their choice of platforms, but shifted from one platform to another adding nest material and soliciting. Occasionally members of a pair seemed to prefer different sites; then the activity of one bird would center around one site while its mate's activity centered around another. One bird of pair 6 (Fig. 5) invited on one platform while its mate was inviting on another. After a few days, activity centered around one site, and this became the definitive nest. I was unable to distinguish the sexes at this time.

The completed nests varied in size and shape with the nest site chosen. Unsupported nests had an iceberg-like form, the great mass of the nest being under water. Nest materials included emergent and submergent vegetation, and sticks. The emergent material utilized was collected from the lake bottom. It was

partially decayed and mixed with bottom sediments. The numbers of nests in which different nesting materials were utilized are shown in Table 1. The nest materials differed with the location of the nest. Pairs nesting in open water used *Potamogeton* spp. while those in emergent vegetation used the species that were most abundant. Pairs nesting in areas where beaver were active used sticks at the base of their nests. Most nest material was gathered within ten meters of the nest site, though I did see a bird from pair 5 in the southwest shore area (Fig. 5) carry a stick approximately 25 meters. As the mound of nest material grew the birds became more careful in their placement of the material and circled the nest before depositing the load. In the final stages of nest building one bird mounted the nest and arranged the material which the other brought to it.

The grebes could build platforms in two to three hours that would support their weight. The period between nest initiation and clutch initiation depended on the number of platforms built, and varied from one day to fourteen days in the southwest shore study area. Some of the delay for those in which the period was long was related to agonistic interactions between pairs.

4.4 Eggs, Clutch Size and Egg Loss.

Newly laid eggs of the Red-necked Grebe are

Table 1. Nest materials used in 78 nests of Red-necked Grebes nesting on Astotin Lake in 1968.

Material	No. of Nests	% of Nests
Sedges	67	85
Grasses	7	9
Cattails	9	12
<i>Potamogeton</i> spp.	31	40
Sticks	11	14
Combination of the Above	33	42

light blue to chalky white in colour. After a few days in the nest the eggs become stained and brown. Variation in size and shape of the eggs is slight. In 1969, 102 eggs from 39 clutches were measured. The results are shown in Table 2. These measurements are similar to those reported by Bent (1919).

Variation between eggs in the same clutch was also slight, the greatest difference in length being 0.7 cm and in width 0.5 cm.

In 1968 nests with newly laid eggs were found on Astotin Lake from May 13 to July 4, while in 1969 they were found from May 4 to July 2. In 1969 initiation dates for 101 clutches in May and June were recorded, and are plotted in Figure 7. Sixty-nine per cent of these clutches were initiated between May 11 and May 31. The average clutch size was 5.2 eggs, ranging from 2-9 eggs. There was a little variation in clutch size in different pairs of the lake as is shown in Table 3. The highest mean clutch size was 5.7, the lowest 4.5. Application of t tests showed that differences in clutch size between areas were not significant (Appendix D). The clutch sizes of 56 nests found in May and June are shown in Table 4 (early nests).

Munro (1941) found a mean clutch size of four on Swan Lake in B.C. He stated that clutches of five were less common, and did not mention clutches larger than

Table 2. Measurements of Red-necked Grebe eggs recorded from Astotin Lake in 1968
and from Bent (1919).

Worker	Sample Size	\bar{x} Length	Range	Centimeters		\bar{x} Width	Range	SD
				SD				
Kevan	102	5.49	5.0-6.0	0.2197		3.57	3.1 -4.0	0.1674
Bent	60	5.37	4.9-6.45			3.45	3.75-3.0	

Figure 7. The initiation dates of 101 Red-necked Grebe clutches found on Astotin Lake in May and June of 1969.

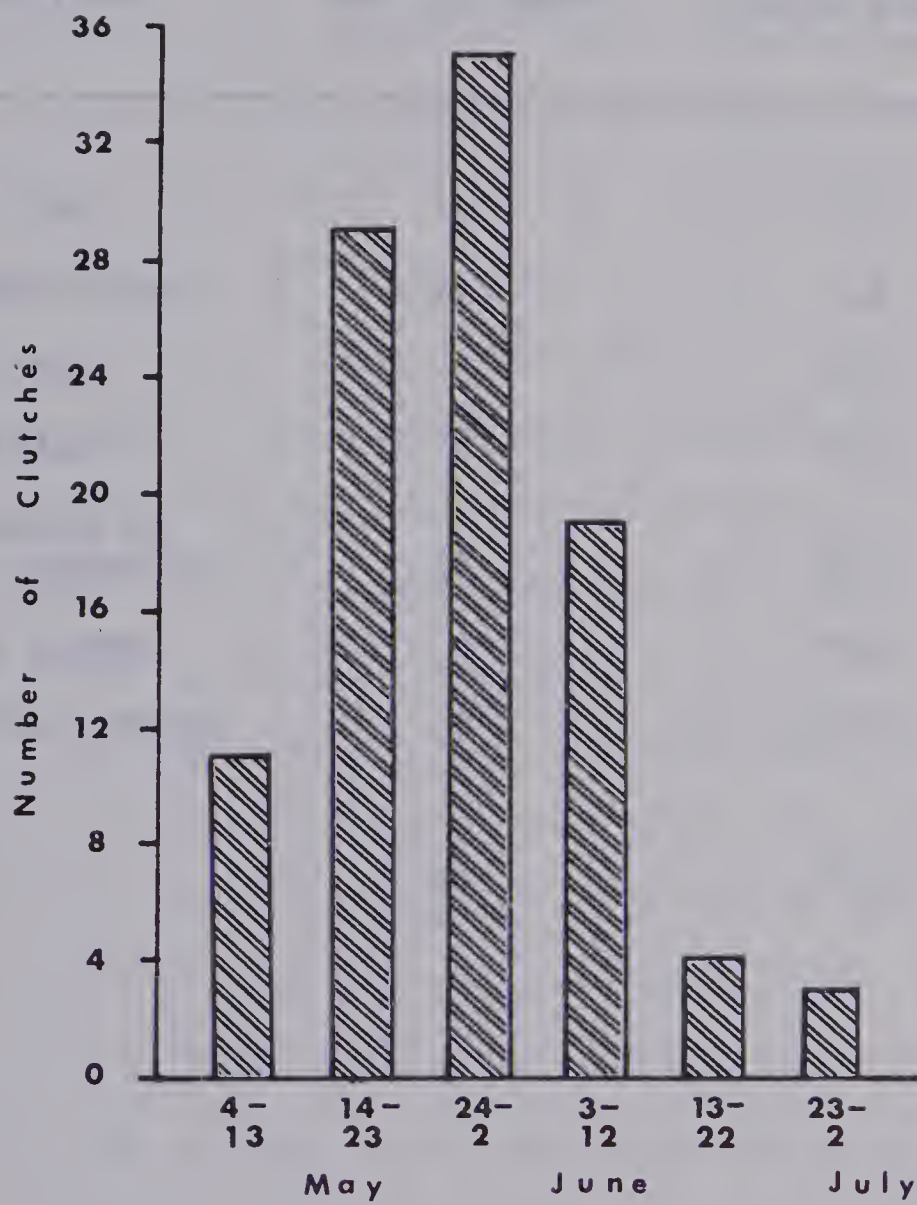


Table 3. Clutch sizes of Red-necked Grebes for different parts of Astotin Lake in 1969.

Area of Astotin Lake	No. of Nests	Mean Clutch Size	Range
Creek Cove	6	5.7	5-8
Northwest Cove	12	4.9	2-7
Martin Bay	6	4.7	3-6
Reed Island	6	4.5	2-7
Cove north of Long Island Pt.	10	5.7	3-9
Willow Clump	6	5.6	4-8
Southwest Shore	8	5.0	3-6
Total	54	5.2	2-9

five. Palmer (1962) stated that the clutch size for the Red-necked Grebe was generally four to five eggs, with occasional clutches of three or six. He stated that larger clutches were the work of more than one female. In both 1968 and 1969 I found clutches of seven and eight eggs. In 1969 in the cove north of Long Island Point (Fig. 1) two clutches of seven eggs and one clutch of nine eggs were found. In 1967 a clutch of thirteen eggs was found in this area (J. C. Finlay, pers. comm.).

It seems to me that clutches produced by more than one female would occur more frequently in areas of high nesting density; however, only two large clutches were found in an area where density was high, for example, in the sedge marshes where nests averaged 11.3 meters apart. The nests with large clutches were usually farther than average from other nests, for example those in the cove north of Long Island Point which were 47 meters apart. This may indicate that grebes nesting farther from other grebes had larger territories which enabled them to feed with less disturbance from neighbouring pairs. Since food supply influences the clutch size of some species of birds (Wallace, 1963) it may have been important for the grebes, too. Correlations between clutch size and age of birds have been found (Lack, 1954) and this may be related to territory size, that is, more experienced birds may hold larger territories.

Unfortunately the ages of the birds in the area were unknown.

Though Red-necked Grebes raise only one brood each season, they renest if they lose their first clutch (Bent, 1919). Since by mid-June in both years most pairs had hatched chicks, nests initiated after this time were considered late nests, and the eggs were presumed to be the second clutch. These second clutches tended to be smaller than the earlier ones. The mean clutch size was 3.1, with a range of one to six for twenty-one clutches in 1969. Eighty-six per cent of the late clutches were in the one to four egg range, while only twenty-nine per cent of the earlier clutches fell in this range (Table 4). During the two summers I found four nests which I felt certain were renests. In 1968 two pairs in Martin Bay (Fig. 1) lost their chicks. These pairs remained on their territories and began re-nesting on July 1. Both pairs had second clutches of three eggs. In 1969 two pairs in the southwest shore deserted their nests. They remained in their territories and renested, one female laying three, the other laying four eggs.

Eggs were lost when they rolled out of the nest, were taken by predators, or deserted. The fates of sixty-eight unhatched eggs in 1969 are shown in Table 5. In 1968 only two eggs were found in the water. In 1969 more thorough searching was done, and twenty-five

Table 4. Clutch sizes of early and late initiated nests of Red-necked Grebes on Astotin Lake in 1969.

Nest Type	Clutch Size								
	1	2	3	4	5	6	7	8	9
Early Nests									
No.	0	2	5	9	18	13	6	2	1
%	0	3.6	9.0	16.0	32.0	23.0	11.0	3.6	1.8
Late Nests									
No.	2	5	6	5	2	1	--	--	--
%	9.5	23.8	28.6	23.8	9.5	4.8	--	--	--
Total Nests									
No.	2	7	11	14	20	14	6	2	1
%	2.6	9.1	14.3	18.2	25.9	18.2	7.8	2.6	1.3

Table 5. The fates of unhatched Red-necked Grebe eggs
found on Astotin Lake in 1969.

Fates of Unhatched Eggs	Number of Eggs	Percent of Unhatched Eggs	* Per cent of all Eggs
Depredated	10	14.7	1.1
Deserted	33	48.5	3.6
Fell in Water	25	36.8	2.7
Total	68	100.0	7.4

*Calculated total. 212 nests (early and late) mean clutch
size of 4.2 eggs.

eggs were found. The contents of twenty-two of these eggs were examined, and twenty-seven per cent of them contained embryos in various stages of development. The others were either infertile or addled. Seventy-six per cent of these eggs were found in two areas of high nesting density, the Northwest Cove, and the cove south of Long Island Point (Fig. 1). It is probable that many eggs lost in the water were not found. Four eggs disappeared from the five manipulated nests in the southwest shore, but were not found in the water. The high loss in the sedge marshes may have been due to two factors: agonistic interactions between pairs, and ducks. An incubating bird disturbed by a threatening neighbour could possibly knock one of its eggs into the water as it hurriedly left its nest. Some of the eggs may have been deserted and subsequently rolled into the water by ducks. Ducks were quite numerous in the sedge marshes and they favored grebe nests for loafing sites.

Egg predation was slight in 1968 and 1969. In 1969 approximately 1.1% of the eggs laid were lost to predators. Over half of the depredated eggs were from nests in rush and reed beds. No mammalian predation was noted. A depredated nest is shown in Figure 8. The eggs were pecked and perhaps partially eaten. It is possible that some of the eggs were pecked by the grebes themselves. This has been reported for Eared Grebes by

Figure 8. A Red-necked Grebe nest found destroyed
at Reed Island in June 1969.



McAllister (1953), but these were "drop" eggs laid before the normal clutch was started. Pecked eggs found on Astotin Lake were in incubated clutches. In two instances Coots were seen near recently depredated nests. Coots have been found to destroy eggs in nests of both Great Crested Grebes (McCarten and Simmons, 1955) and Red-necked Grebes (Wobus, 1960).

In 1969 thirty-three eggs from twenty deserted nests were found. Twenty-two of these eggs were found in nests in sedge marshes, most of them being in nests from which chicks had been reared. The average number of eggs deserted was 1.6 per nest. Tristham (in Pike, 1913) suggested that the Great Crested Grebe hatches two chicks and then deserts the remaining eggs to care for the young. Welty (1966) interprets this phenomenon as the feeding instincts overpowering the brooding. Since most deserted nests (70%) on Astotin Lake were found in areas of high breeding density, agonistic interactions between pairs could have caused much of the desertion (see Section 4.8).

4.5 Incubation, Hatching, Chick Loss and Brood Size.

In nests under observation along the southwest shore the incubation period began with the first egg and continued for 23 days. This incubation period agrees with the 22 to 23 days recorded for eggs hatched artificially.

Both members of the pair took turns incubating.

In 1968 the peak in hatching on Astotin Lake was between June 16 and June 25. In 1969 most of the chicks hatched between June 1 and June 20. The eggs in nests along the southwest shore hatched at two day intervals, occasionally daily intervals. McAllister (1963) reported a brood of six Red-necked Grebes hatching in two days.

The Red-necked Grebe chick begins cheeping in the egg between 12 and 36 hours before hatching (McAllister, 1963). The hatching process itself is very short: in an incubator the time between first pipping and hatching is from 50 minutes to 2 hours (McAllister, 1963).

In both 1968 and 1969 dead chicks were found floating in the lake in June and July. From the sizes of the chicks they were estimated to range in age from 1 day to 4 weeks. One small chick was found dead on the nest and was presumed to have died of exposure (July 18, 1968); its down had never dried. Nineteen chicks were found in all, ten of them in 1969. I examined the stomach contents of eleven chicks (Appendix C.) Three were autopsied by the Veterinary Services Division of the Alberta Department of Agriculture, and three were examined for parasites by Mr. J. W. Wolford of the Zoology Department of the University of Alberta. All of the birds examined for parasites contained small trematodes

[echinostomes, and *Ribeiroia* sp.] and cestodes [*Schistocephalus* sp.] None of the infestations were considered abnormal (Wolford, pers. comm.). Two of the birds examined by Veterinary Services were found to have a septicemic disease; staphylococcal bacteria were isolated from cultures of the heart and liver of the birds. There was no evidence of this disease in the third bird. Diseases of this type can be fatal. How much mortality the disease caused is uncertain.

In 1968 a pecked chick was found on a depredated nest. No other evidence of chick predation was found. Pike (*Esox* spp.) have been reported to be the chief predator of young grebes (Harrison and Hollom, 1932), but there are no pike in Astotin Lake. Avian and mammalian predators are abundant. Presumably predators taking grebe chicks would also take ducklings. The mean brood size of Mallards (*Anas platyrhynchos*) on Astotin Lake in 1969 was 10 while the mean clutch size for these birds was 8.04 in the Miquelon Lake region to the south (Long, pers. comm.). This may reflect little predation on ducklings, and the same may be true for grebes.

The mean brood sizes for Red-necked Grebes in 1968 and 1969 were not significantly different (t test, $P > 0.05$) being 2.2 and 1.8 for each year respectively. The mean for 1969 agrees exactly with that found by Munro (1941) on sixteen lakes in British Columbia for

the years 1936 - 1941. The brood sizes for 1968 and 1969 are compared with those of Munro in Table 6. Small brood sizes have also been reported for the Great Crested Grebe (Simmons, 1955) and the Black-necked Grebe (*Podiceps caspicus*) (Hanzak, 1952). Simmons (1955) found that the brood size of the Great Crested Grebe varied from pond to pond, and felt that smaller broods on some ponds were due to predation.

The small brood sizes on Astotin Lake can not be accounted for by known egg and chick losses. The mean loss was 3.4 potential grebes (65%) while the known losses accounted for only 6.2% (Table 5). Obviously not all losses were noticed, particularly chick losses. Two chicks disappeared in the southwest shore soon after hatching; they were never found despite extensive searching. Newly hatched chicks may be crushed on the nest when the parents return to incubate or they may die of exposure while parents are feeding siblings. Chicks dying in the nest are probably carried away by the adults. Chicks may be separated from their parents by boaters chasing the birds, but brood size was small in areas not frequented by boaters, too. Disease may take a high toll. It seems unlikely that any one factor is the main cause of small brood sizes.

4.6 The Nesting Habitat.

One of the requirements for a nest site on

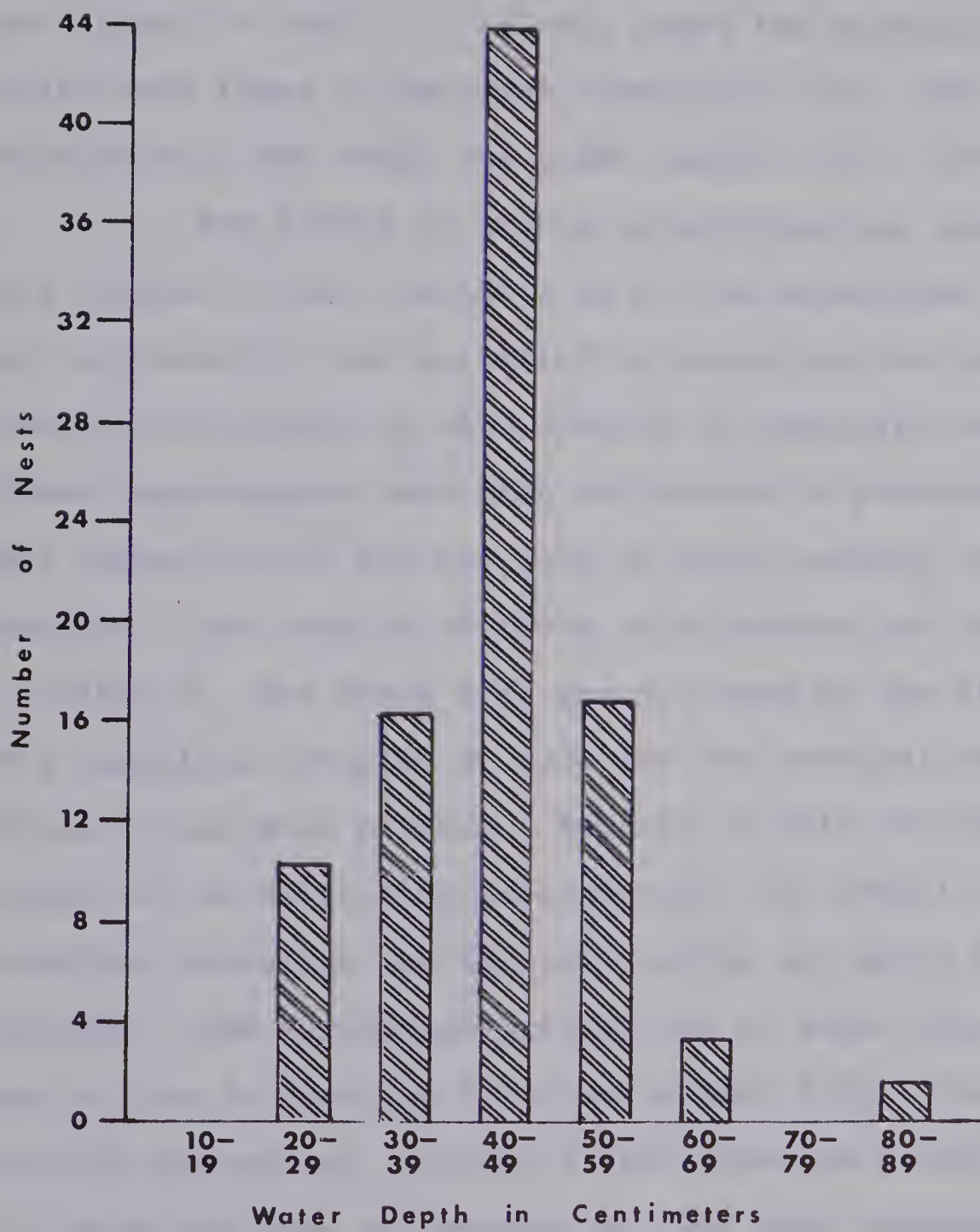
Table 6. A comparison of brood sizes of Red-necked Grebes found on Astotin Lake with those found in British Columbia by Munro (1941).

Worker	Year	No. of Pairs	No. with- out Chicks	No. With Chicks	Brood Size					\bar{x} brood pairs with chicks	\bar{x} brood all pairs
					1	2	3	4	5		
Kevan	1968	18	?	18	6	7	4	0	1	2.1	?
Kevan	1969	89	37	52	25	16	8	2	1	1.8	1.1
Munro	1936-1941	35	?	35	11	19	4	1	0	1.8	?

Astotin Lake was easy access to water of swimming depth. All the sites were in or immediately surrounded by water deep enough for the birds to swim in; most were in or by water deep enough for the birds to dive in as well. The number of nests found at various water depths is shown in Figure 9. At Astotin Lake the mean water depth at nest sites in May of 1969 was 42 cm , with a range of 20 to 81 cm. Although Western Grebes have been known to nest on dry land (Nero, et al, 1958) this was not the case for Red-necked Grebes on Astotin Lake. Three nests in water 20 cm deep were stranded because of a drop in water level. They were subsequently deserted and new nests assumed to belong to the same pairs were found in deeper water near the nests. It was assumed that the nests were deserted because the birds could no longer swim to them.

Gotzman (1965) reported that 90% of the Red-necked Grebes in his study area in Poland nested in water 50 cm or more in depth. Bent (1919) found grebes nesting in water three or four feet deep (91.5 to 132 cm). The variability of nest site water depth is probably related to the contours of the lake basin and the type of cover available. On Astotin Lake areas deeper than 65 cm were usually in open, unprotected parts of the lake (Fig. 1) though water in the reed and rush beds used by the grebes was sometimes deeper than this. The shallow protected bays were used extensively by nesting grebes.

Figure 9. The number of Red-necked Grebe nests found at various water depths on Astotin Lake in May and early June of 1969.



The nesting habitat of the Red-necked Grebe can be divided into three types: emergent vegetation, shallow open water, and supporting objects. The habitats and the number of nests found in each in 1968 and 1969 are listed in Table 7. In both years the majority of the nests were found in emergent vegetation (67 - 70%) particularly the sedge and grass marshes (54 - 58%).

The number of grebes using shoreline vegetation was related to the availability of the vegetation. Habitat availability was estimated by measuring the amount of shoreline occupied by each species of shoreline vegetation. These measurements were then calculated in percentages and compared with the per cent of pairs nesting in each habitat. The results of these calculations are shown in Table 8. The beach area was not used by the birds. The shoreline occupied by woodland was used only when fallen trees were present. Because of this utilization could not be calculated meaningfully, the amount of woodland shoreline and the utilization not being directly related. The percentage utilization of sedge and grass, and willow for nesting sites was almost triple the availability percentage. Cattails and rushes were utilized in about the same percentages as they were available.

The vegetation differed in density and this was found to influence utilization. The vegetation was classed according to the definitions of density presented

Table 7. Nesting Habitats utilized by Red-necked Grebes in 1968 and 1969 on Astotin Lake.

Habitat Type	Habitat	1968		Utilization		1969	
		No.	%	No.	%	No.	%
Emergent Vegetation	Sedge and Grass	63	54.8	123	58.0		
	Cattail	14	12.2	12	5.7		
	Reeds	?	?	9	4.2		
	Rushes	?	?	6	2.8		
Supporting Objects	Willow	13	11.3	18	8.5		
	Fallen Trees	6	5.2	6	2.8		
	Beaver Caches	3	2.6	4	1.9		
	Mud Flats	0	0	4	1.9		
Shallow Open Water	Open Water	16	13.9	30	14.2		
Total		115	100.0	212	100.0		

Table 8. The per cent of shoreline habitats available and their usage as nesting sites for Red-necked Grebes on Astotin Lake.

Shoreline Habitat	% Available on Lake	Nest Sites Utilizing Habitat 1968			Habitat 1969			Both Years	
		No.	%	No.	No.	%	No.	%	
Sedge and Grass	29.2	63	75.0	123	186	80.5	186	78.4	
Cattail	6.9	14	16.6	12	26	7.8	26	11.0	
Rushes	5.8	--	--	6	6	3.9	6	2.5	
Willow	5.3	7	8.4	12	19	7.8	19	8.1	
Woodland	49.3	--	--	--	--	--	--	--	
Beach	3.5	--	--	--	--	--	--	--	
Total	100.0	84	100.0	153	237	100.0	237	100.0	

by Gotzman (1965).

full density: the emerged parts of the plant are in contact with each other, forming a dense compact thicket very difficult to force one's way through.

great density: emerged portions of the plants are not in contact with each other, but a man finds it rather difficult to go through; leaves a distinct trace behind him in the form of a belt of destroyed vegetation.

medium density: it is possible to walk through without any difficulty, a trace will, however, remain behind.

loose density: patches of open water surface are found between individual plants or their clumps, walking is possible with no difficulty or damage to vegetation.

In the sedge and grass marshes the vegetation was growing in hummocks and was classed as loose density vegetation. Willow was also in this classification. Cattail grew only at full density and at loose density, while rushes and reeds grew from loose to great density. Nests in cattail were found only in vegetation of loose density. When the amount of cattail growing at loose density was calculated, the utilization was found to be 3.6 times the availability. Nests in reeds and rushes were found in vegetation of medium density. Because of the variation of density in different parts of the rush beds, I was unable to calculate the availability of rushes growing at medium density. Rushes were the primary vegetation in Gotzman's study area, and he found that 80% of the Red-necked Grebes nested in medium density vegetation.

The distance from nests in emergent vegetation to open water was measured. The majority (83%) of the nests in the sedge marshes were found closer to open water than to shore: the mean distance to open water was 4.0 meters with a range of 0.3 to 15.5 meters. Nests in the rushes tended to be farther from open water, the mean distance being 6.1 meters with a range of 1.5 to 12.0 meters. Nests with loose density vegetation between them and open water tended to be farther from open water than those separated from it by medium density vegetation. No correlation was found between distance to open water and nesting success, though presumably those nests close to open water would suffer more from wave action than those farther into the zone of vegetation.

The mean distance to shore in the sedge marshes was 10.6 meters with a range of 1.8 to 27.4 meters. Nests closer to shore tended to be in shallower water and were more subject to stranding and subsequent desertion. Work on Pied-billed Grebes has shown that nests closer to shore are more subject to predation (Glover, 1953). Due to the low predation on Astotin Lake, I was unable to investigate the relationship between predation and distance of the nest from the shore.

The sedge marshes graded from loose density near open water to full density at the shore. No significant differences were found between vegetation densities

near nest sites and at random points in the marsh where the vegetation grew at loose density (Appendix F). In the marsh of the cove south of Long Island Point, the mean distance between hummocks was 2.0 meters, while the mean hummock area was 0.19 square meters. Within the marsh the birds tended to select sites beside hummocks. Sixty-seven per cent of the nests were beside hummocks, and most of these nests were between two or more hummocks. The hummocks provided nesting material and anchoring sites for the nests, protected them from wave action, and hid them.

Fourteen per cent of the 212 nests found in the summer of 1969 were in open water. Thirty per cent of these nests were found in sheltered bays and inlets in May. The water at these sites tended to be deeper ($\bar{x} = 52.5$ cm) than nests in the marshes. Seventy per cent of the open water nests were established toward the end of June. Many of these late nests were suspected to be renests because equal numbers of old nests were found nearby in the marshes.

Nests in unsheltered areas sometimes came adrift or rapidly disintegrated or both. In late June of 1969 two nests in open water were moved over 30 meters by a storm. The nests were deserted after the storm even though the eggs were undisturbed. The second nest of pair 7 in the southwest shore (Fig. 5) disappeared after

a July rainstorm. Late in the season many open water platforms were found that disappeared within a week's time. They were probably destroyed by wave action.

The fact that open water nests are more prevalent late in the nesting season after the water level has dropped in the marshes may indicate that open water sites are less suitable. If this is so, those birds nesting in open water early in the season may have been birds that were unsuccessful in competing for nest sites in more suitable areas. Observations using marked birds would have to be made before this could be confirmed.

Supporting objects for nest sites included willow stumps, fallen trees, beaver caches, and mud flats. Fifteen per cent of the nest sites in 1969 were of these types. Willow was the most abundant site of this type and the most used. Willow was found in patches along the shoreline and in a clump between Long Island and the west shore of the lake (Fig. 1). Six nests were found in this clump each season. The mean distance between nests was 9 meters, with a range of 3 to 12 meters. The elliptical shaped clump was 28 meters long and 20 meters wide. The nests were found around the outside of the clump, and were usually anchored in the crotch of the willow stumps.

In each season six nests were supported by the branches of fallen trees. The trees used were close to

nest material, either submergent or emergent vegetation.

Four nests in 1969 were found on beaver food caches. They were built of emergent or submergent vegetation and rested on the partially submerged branches that the beavers had stowed near their lodge. Not all such caches were used by the grebes. Those not used seemed to lack close access to nest material.

In 1969 four nests were found on small mud flats. These mud flats had water on all sides. The nests were located at the edge of the flats so that the distance to water of swimming depth was only a few centimeters, and the birds did not have to walk to their nests.

From the above results three things seem to be essential for the nesting of the Red-necked Grebes: easy swimming access to the site, nest material close to the site, and protection from wave action. All successful nest sites on Astotin Lake had these three characteristics in one form or other. No nests were found in vegetation too dense to swim through easily. All successful nests were in or surrounded by water deep enough to swim in. Nest material in the form of emergent or submergent aquatic vegetation was close to each nesting site.

Protection from wave action was afforded in two main ways. Eighty-six per cent of the sites provided a means of anchoring the nest so that it could not drift. The nest material was either woven into emergent

vegetation or the nest was situated in the vegetation in such a way that it was almost surrounded by the vegetation. Fifteen per cent of the sites provided support beneath the nest as well as anchoring places. These sites included fallen trees, beaver caches, willows, and mud flats. By providing a solid base for the nest these sites protected the nest from wave action.

4.7 Agonistic behaviour of the Red-necked Grebe.

Agonistic interactions noted in the southwest shore study area included Threat, Token Diving, "Standoffs" and Fighting. Threat was divided into two categories: High Threat and Low Threat (Wobus, 1964). Low Threat (Fig. 10 a) occurred in two forms. When used against other Red-necked Grebes the neck was bent so that the head was close to the body. This posture is the same as the threat of the Horned Grebe illustrated in Storer (1969) and was most frequently used between bouts of Token Diving. When Low Threat was used against birds of another species, the neck was usually extended and the approach sometimes ended in a shallow dive in which ripples marked the progress of the threatening bird. The High Threat (Fig. 10 c) was used in interactions when the birds were only a few body lengths apart. There seemed to be a gradation between Low Threat, High Threat, and Appeasement (Fig. 10 a-e). Generally, the closer the threatening

birds were to each other the higher the threat. In some cases the postures assumed seemed to be part Appeasement and part threat. I termed such postures as "Standoff" postures (Fig. 10 d). In this posture the body feathers were sleeked, the tail cocked and the head held high with the bill pointing slightly upward. Birds assuming this posture usually swam very slowly, circling each other about a body length apart. Frequently there were three or four birds involved in this circling. Such encounters generally ended with the birds drifting apart, joining their mates, and swimming off calling. On two occasions, I saw "Standoffs" end in fighting.

Token Diving is known in the Great Crested Grebe and the Red-necked Grebe (Storer, 1969). Token Dives observed on Astotin Lake began with the bird assuming a Low Threat posture. While in this posture the bird dove. The dive was short, and the bird tended to stay in the same place. Token Diving was used only against other Red-necked Grebes. It was usually used when a grebe did not retreat after other forms of threat. On two occasions, I saw a Token Dive develop into a underwater attack resulting in a fight.

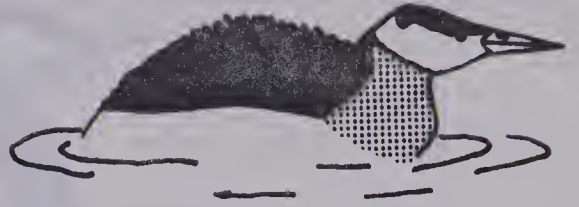
Fights were rarely longer than four or five seconds. They began with the birds lunging at each other, or by one bird diving and coming up under the other. Fighting birds jabbed with their beaks, kicked with their feet

Figure 10. Agonistic postures of the Red-necked Grebe taken from photographs of the birds in the southwest shore area of Astotin Lake.

- a. Low Threat
- b. Threat intermediate between High and Low threat
- c. High Threat
- d. "Standoff"
- e. Appeasement
- f. Triumph Ceremony



a



b



c



d



e



f

and pounded each other with their wings. In prolonged fighting the birds grappled with their beaks and forced each other under water. Such fights usually attracted the mates of the birds. In two such encounters the mates of the birds began fighting with each other.

After a fight or "Standoff" the birds involved turned to their mates and the pairs swam toward their nests calling. I called this ceremony a "Triumph Ceremony" (Fig. 10 f) because of its similarity in occurrence to the Triumph Ceremony of the Horned Grebe (Storer, 1969). The posture differed from that of the Horned Grebe in that the head was held higher.

The Appeasement posture (Fig. 10 e) was very similar to that described for the Horned Grebe (Storer, 1969) and the Eared Grebe (McAllister, 1958). In this posture the head and body feathers were sleeked, the tail was cocked, and the head was held high with the bill parallel to the water. The head was held slightly back so that the shape of the bird resembled the letter "Z".

4.8 Territory Establishment and Agonistic Interactions.

Territories were established along the southwest shore between May 4 and May 21, 1969 (Table 9). The pairs did not use the artificial nest sites for nesting although they did investigate them and used them for copulation. On May 2 there was one pair in the area. By May 7

Table 9. Nesting data for pairs establishing in the southwest shore area of Astotin Lake in 1969.

Pairs	Arrival Date	Establishment Date	No. of Nest Sites Examined	Distance to Nearest Neighbour at Establishment	Clutch Initiation Date	Clutch Complete	Clutch Size	Hatching Success
1	May 2	May 4	2		May 8	May 17	6	3
2	?	May 7	3	3 m	May 22	June 2	6	4
3	?	May 7	2	3 m	May 21	May 30	5	deserted
4	May 7	May 12	4	16 m	May 18	June 1	6	1-deserted the others
5	May 12	May 18	3	28 m	May 24	June 2	5	4
6	May 13	May 19	3	6.3 m	May 28	June 3	4	4
7	?	May 21	1	20 m	June 5	June 12	5	deserted

there were six pairs in the area, and three of these had established nest sites. The nest sites and areas defended by pairs 1, 2, and 3 are shown in Figure 11. The unestablished pairs were mobile, drifting in open water about 20 meters from the shore. Rarely would more than one pair linger in the area very long. Those that did performed Head Shaking and Weed ceremonies. Often after a Weed ceremony one of the pair solicited by Inviting in open water. The pair then approached the sedge marsh and were threatened by established pairs. The response to threatening was variable. Sometimes the new pair withdrew slowly. Occasionally they threatened as well and brief scuffles between the defending bird and the new pair ensued. The new pair probably had to win a few of these fights before they could enter the nesting ground. This is not certain however. As the new pairs settled, the territories of the previously established pairs shifted (Figs. 11, 12, 13).

The territorial behaviour of the established pairs prevented or delayed the establishment of other pairs. If all six pairs seen in the area on May 7 settled in the marsh, pair 4 was delayed 5 days, and pairs 5 and 6 were delayed 11 and 12 days respectively (Table 9). In all cases 2 days elapsed between the time a pair was seen in a particular area near the marsh and the time a pair (presumably the same one) began building a platform in the

Figure 11. The nest sites and areas defended in the southwest shore area of Astotin Lake by Red-necked Grebe pairs 1, 2, and 3 on May 7, 1969.

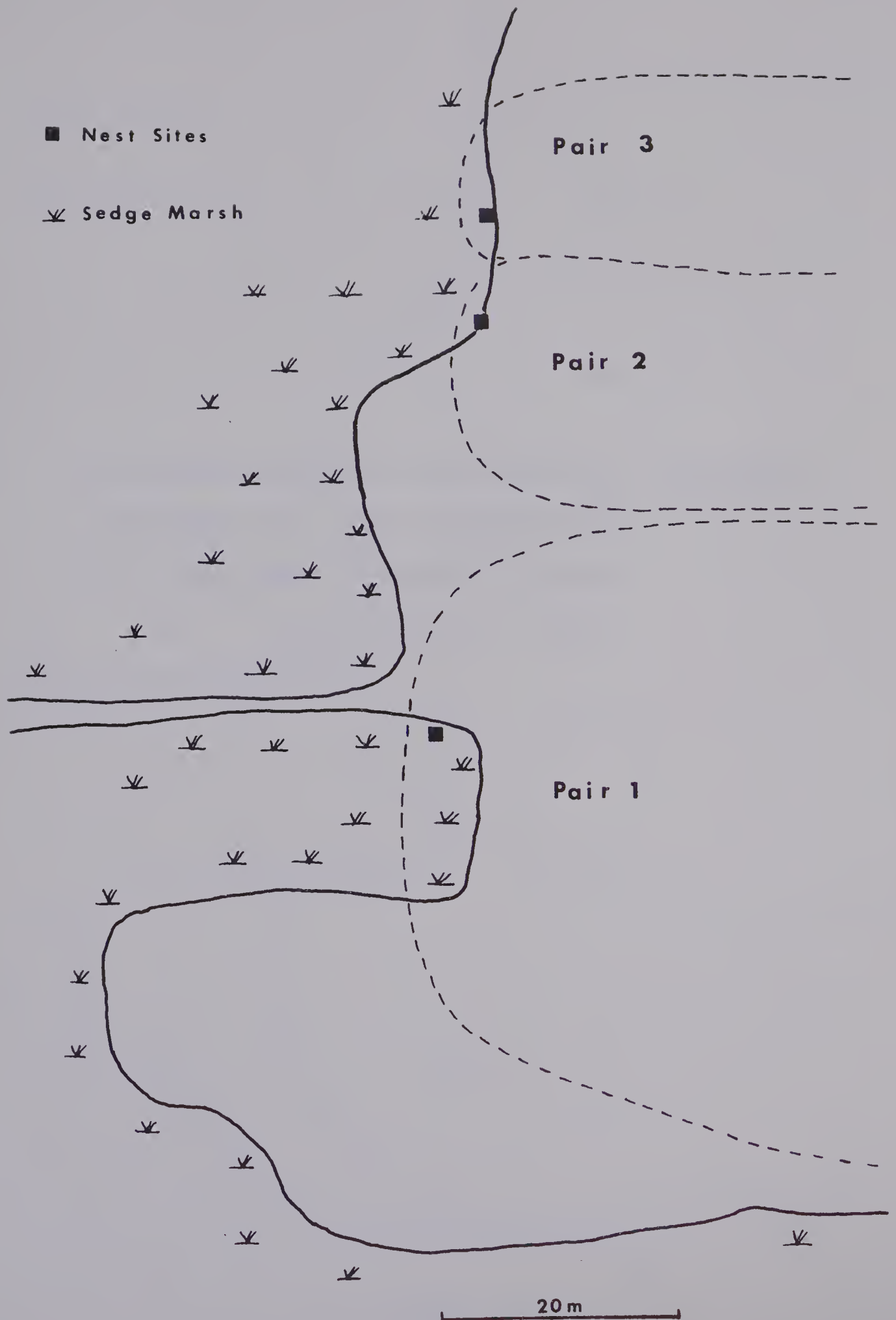


Figure 12. The nest sites and areas defended in the southwest shore area of Astotin Lake by Red-necked Grebe pairs 1, 2, 3 and 4 on May 14, 1969.

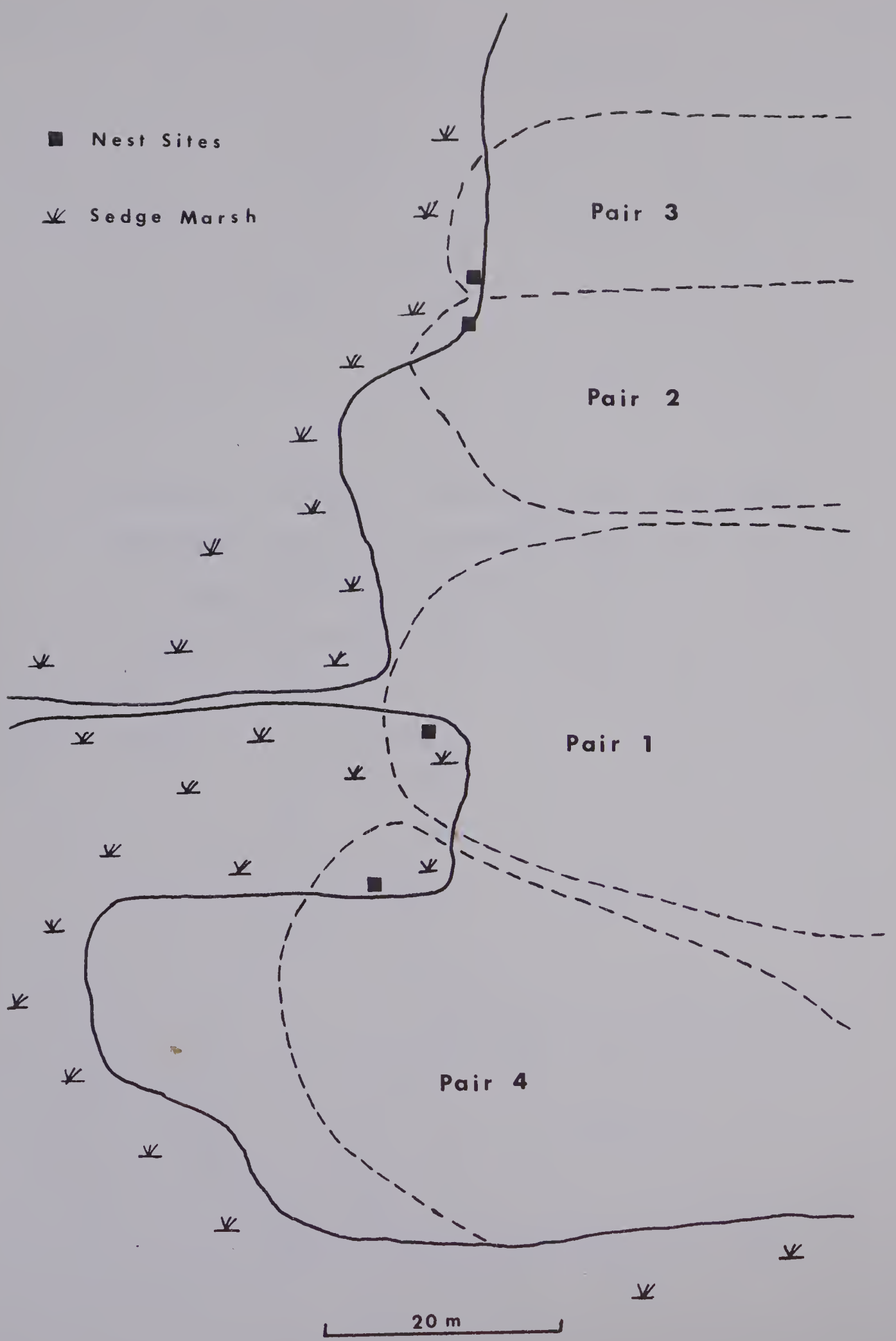
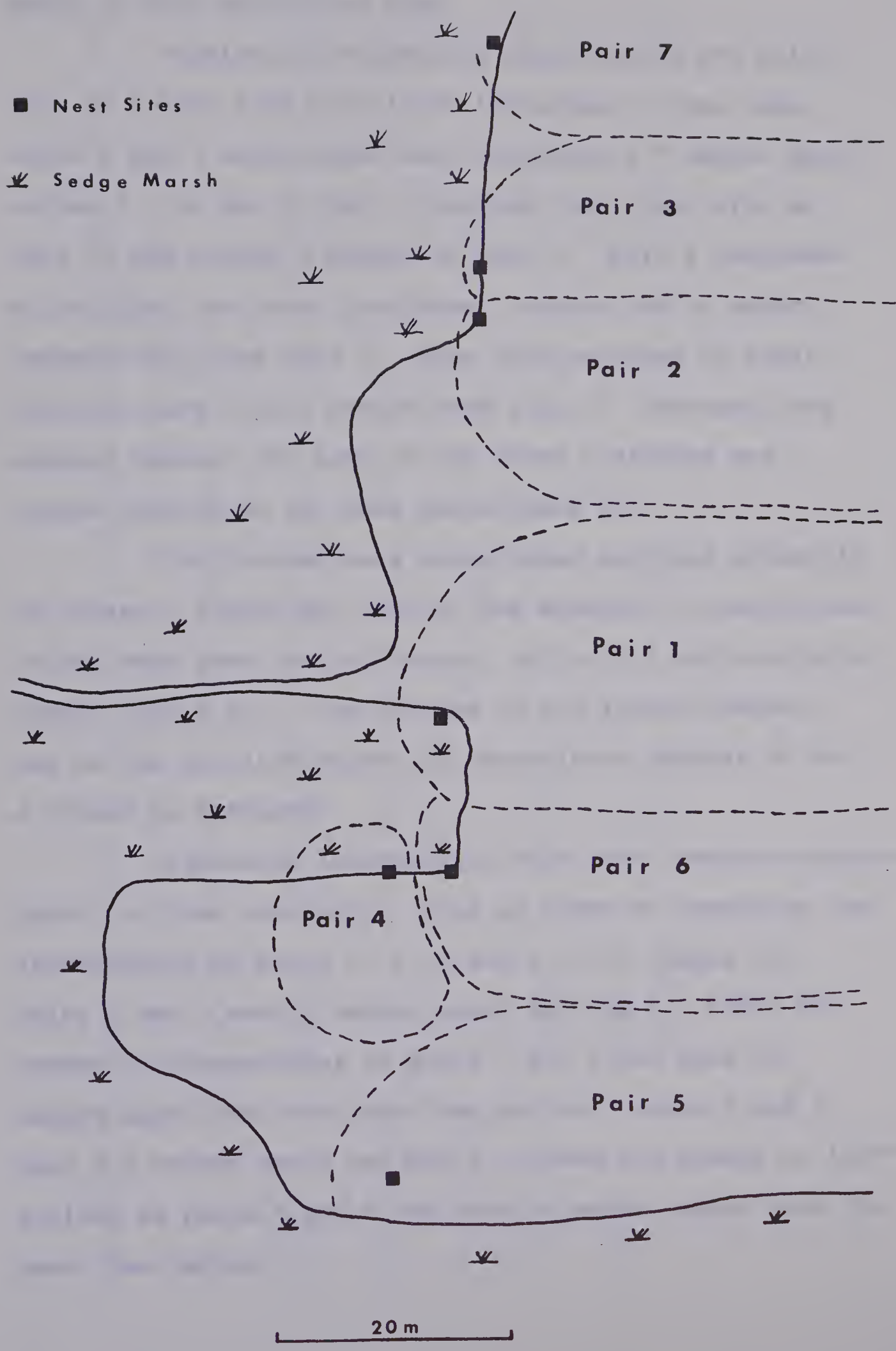


Figure 13. The nest sites and areas defended in the southwest shore area of Astotin Lake by Red-necked Grebe pairs 1, 2, 3, 4, 5, 6 and 7 on May 22, 1969.



marsh in that particular area.

Agonistic interactions also delayed the selection of a nest site and clutch initiation in one case. Pairs 2 and 3 established nest platforms 6.7 meters apart on May 7. On May 14 pair 3 shifted their nest site so that it was within 3 meters of pair 2. Pair 2 responded by building two other platforms 6 meters and 19 meters respectively from pair 3. They then returned to their original nest site 3 meters from pair 3. Fourteen days elapsed between the date of the first platforms and clutch initiation for both pairs (Table 9).

Territories were established and held primarily by threat. Eighty per cent of the agonistic interactions in May were some form of threat, while 13.2 per cent were fights (Table 10). The outcome of the fights however, may be the decisive factor in determining whether or not a threat is honoured.

Agonistic interactions were most numerous between pairs in close proximity. This is shown by examining the interactions of pairs 1, 2, 3 and 4, 5, 6 (Table 11). Pairs 2 and 3 were 3 meters apart and had 5.3 times the number of interactions as pairs 1 and 2 who were 38 meters apart over the same time period. Pairs 4 and 6 were 6.3 meters apart and had 6.1 times the number of interactions as pairs 5 and 6 who were 30 meters apart over the same time period.

Table 10. The number and type of agonistic interactions in May and June, 1969 between seven pairs of Red-necked Grebes in the southwest shore study area of Astotin Lake. Figures in parentheses are percentages.

Month	Threats	Token Dives	Standoffs	Fights	Chases	Chase Other Species
May	110	85	30	37	5	14
	(39.1)	(30.3)	(13.2)	(13.2)	(1.8)	(4.9)
June	178	70	86	50	42	25
	(39.5)	(15.5)	(19.1)	(11.1)	(9.3)	(5.5)
Total	288	155	116	87	47	39
	(39.3)	(21.2)	(15.9)	(11.9)	(6.4)	(5.3)

Table 11. The number of agonistic interactions between pairs of Red-necked Grebes in the southwest shore area of Astotin Lake during the month of May, 1969.

Pairs	1-2	1-4	1-5	1-6	2-3	2-7	3-7	4-5	4-6	5-6
Distance between Pairs	38 m	16 m	44 m	14 m	3 m	23 m	20 m	28 m	6.3 m	30 m
Hours of Observation	28.5	28.5	24.4	15.0	28.5	12.7	12.7	24.4	15.0	15.0
No. Of Agonistic Interactions	6	17	--	8	32	9	9	21	61	10
Agonistic Interactions per hour	0.21	0.60	--	0.53	1.1	0.71	0.71	0.86	4.1	0.67

The location of the nest site in the marsh also affected the number of interactions. The interactions of pairs 4 and 6 were 1.9 times those of pairs 2 and 3 even though the nests of 2 and 3 were closer together. The nest of pair 4 was in an inlet, and the pair had to swim past the nest of pair 6 to get to their nest (Fig. 13). Pairs 2 and 3 nested along the shore and had free access to open water without going near each others nests. Presumably the interactions between pairs 4 and 6 were greater because pair 4 had to pass through or near the territory of pair 6 to get to its nest.

4.9 Nest Site Manipulations.

Pairs 2 and 3, and 4 and 6 responded differently to cutting sedge at the nest site. For pairs 2 and 3 agonistic interactions after removing the sedge were 3 and 4 times those in May (Table 12). The absence of the sedge seemed to increase the number of interactions between the pairs. Cutting the sedge between 4 and 6 had little effect on the number of agonistic interactions between the pairs (Table 13). If the vegetation does have a shielding effect which reduces interactions, it does not work with all pairs. There may be no shielding effect at all. The increase in interactions between pairs 2 and 3 may have been caused by confusion resulting from the removal of landmarks rather than by the loss of the shielding effect of the vegetation.

Table 12. The number of agonistic interactions between Red-necked Grebe pairs 2 and 3 during nest site manipulations in June of 1969 in the southwest shore study area of Astotin Lake.

Date	Manipulation	Threats			Fights			Total			Hr. Ob.	Interactions /Hr.		
		2	3		2	3		2	3			2	3	
May	None	27	27		5	5		32	32		28.5	1.1	1.1	
June 2	Cut Sedge at 2 & 3	9	6		2	2		11	8		2.3	4.8	3.4	
June 3	All Sedge cut at 2 & 3	5	5		0	0		5	5		1.2	4.1	4.1	
June 7	None	4	4		0	0		4	4		2.0	2.0	2.0	
June 8	2 towards 3 2 m apart	4	4		1	1		5	5		4.4	1.1	1.1	
June 10	2 towards 3 1 m apart	5	5		0	0		5	5		4.0	1.3	1.3	
June 11	2 towards 3 30 cm apart	8	8		1	1		9	9		4.5	2.0	2.0	
June 12	2 towards 3 in contact	20	18		4	4		24	22		7.0	3.4	3.1	

Table 13. The number of agonistic interactions between Red-necked Grebe pairs 4, 5, and 6 during nest site manipulations in June, 1969 in the southwest shore study area on Astotin Lake.

Date	Manipulation	Threats			Fights			Total			Hrs. of Obs.			Interactions/Hr.		
		4	5	6	4	5	6	4	5	6	4	5	6	4	5	6
May	None	78	29	68	4	2	3	82	31	71	24.4	24.4	15	3.4	1.3	4.7
June 7	Cut Sedge at 4.6	11	4	11	0		0	11		11	2.6	2.6	2.6	4.2		4.2
June 8	None	16		16	2		2	18		18	4.4	4.4	4.4	4.1		4.1
June 10	None	19		19	1		1	20		20	4	4	4	5		5
June 11	6 towards 4 5 m apart	8		8	3		3	11		11	4.5	4.5	4.5	2.4		2.4
June 12	5 towards 4 18 m apart	7	4	7	0	0	0	7	4	7	7	7	7	1.0	.5	1.0
June 16	4 towards 6 4 m apart	14	2	9	1		1	15	2	10	4	4	4	3.8	.5	2.5
June 17	6 towards 4 1.5 m apart	3		3	1		1	4		4	2.3	2.3	2.3	1.7		1.7
June 19	4 + 6 in contact 5 towards 4 9.3 m apart	21	4	21	3	0	3	24	4	24	3.4	3.4	3.4	7.1	1.1	7.1
June 20 am	5 towards 4 m apart 4+6 3 m apart	8	4	4	0	0	0	8	4	4	1.5	1.5	1.5	5.3	2.7	2.7
June 20 pm	5 towards 5 2.6 m from 4 2.8 m from 6	25	21	23	1	2	1	26	23	24	2.1	2.1	2.1	12.4	10.9	11.4
June 24	5+6 1.3 m apart 5+4 1 m apart	13	19	10	3	0	3	16	19	13	3.5	3.5	3.5	4.6	5.4	3.7

The pairs responded differently to nest moving. On two occasions pairs refused to move with their nests. Pair 7 accepted a move that placed their nest 3.5 meters closer to pair 3, but did not accept another move of 1.3 meters. They deserted the nest even though it was replaced to its original position after two hours.

Pair 4 did not accept a move which placed them 1 meter closer to pair 6. Instead they continually returned to the place where the nest had been, and began building another nest. The behaviour of pair 4 may have stemmed from submissiveness to pair 6 or fidelity to the nest site. The behaviour of pair 7 seemed to indicate submissiveness to pair 3 since they did accept one move, but would not accept another shorter one.

In three cases of nest moving (pairs 2, 6 and 5) the pairs involved moved with their nests and their territories shifted accordingly. With pairs 2 and 6 when the nests were moved the interactions between the pairs dropped or remained the same as they were in May (Tables 12 and 13). The birds whose nests were moved were less aggressive than usual while the birds whose territories were being invaded did not initiate more interactions. Interactions increased slightly after the pairs had habituated to the new nest site (Tables 12 and 13). Both threats and fights increased when the nests were placed side by side. Both pairs 2 and 3,

and 4 and 6 incubated side by side, however. The nests of pairs 2 and 3 were left side by side for two days. Pair 2 adopted the nest of pair 3. When the nests were separated pair 2 continued to incubate the eggs in the nest of pair 3 and forced pair 3 to desert. Pair 3 renested in open water 27 meters from their former nest site. Evidently pair 2 was dominant over pair 3.

The interactions of pair 5 with their neighbours increased steadily during nest manipulation (Table 13). Their territory shifted with their nest site and they defended an area halfway between their nest and the nests of 4 and 6. Pair 5 readily chased the members of pair 4. They initiated fights with both pairs 4 and 6. On June 24 pair 5 swam into the territory of pair 6 and adopted the day old chick of pair 6. The male of 6 fought briefly with the male of 5, but the female of 6 remained on the nest incubating while the chick climbed up on the back of the female of pair 5.

Evidence of a developing dominance hierarchy noted throughout the manipulation period, particularly with pairs 4, 5, 6, and 1. Pair 4 became the subordinate pair. Members of pairs 5, 6 and 1 chased pair 4. Pair 4 began approaching and leaving their nest under water. After nest relief the relieved bird would swim out to open water rather than staying near the nest. This meant that the incubating bird was subject to harassment from

the other pairs. Both members of pair 6 frequently approached the nest of 4 and frightened the incubating bird off the nest. After nest 5 was moved closer to 4, pair 4 began approaching and leaving their nest by going through the sedge and passing through the territory of pair 1. By doing this they were chased by only one pair rather than two.

At first, encounters between 5 and 6 indicated that the pairs were equally dominant. There were numerous threats and fights initiated by both pairs. Within 10 days birds from 6 were assuming the Appeasement posture when approached by birds from 5. Once a bird from pair 5 chased a bird from pair 6. Pair 5 successfully adopted the chick of pair 6. The relationship between pairs 5, 6, and 1 was not clear. Early in the season both pairs 5 and 6 were chased by pair 1. In June the three pairs had few encounters. With pairs 4, 5, and 6, pair 5 was dominant, while pair 4 was subordinate. Pair 6 was dominant over pair 4 but subordinate to pair 5.

Territories in the southwest shore differed in size and type. Nice (1943) defined six types of territories:

- A. Mating, nesting and feeding
- B. Mating and nesting but not feeding
- C. Mating station only
- D. Nesting station restricted to the narrow surroundings of the nest
- E. Feeding territories
- F. Roosting territories

Simmons (1955) found that Great Crested Grebes usually hold type B territories, although some hold type A and others hold type D territories. At the southwest shore area pair 1 had a type A territory of approximately 140 m² which they held for 4 weeks after the chicks had hatched. Pairs 2 - 6 held type B territories and fed in the open water 50 meters from the nest sites. During nest site manipulation the territory of pair 4 became a type D territory of approximately 1 m². After one chick hatched the pair deserted.

5. Concluding Summary and Discussion.

Red-necked Grebes arrived at Astotin Lake in late April. Some of the pairs seemed to be paired on arrival because they immediately established territories and began nest building and copulating. Other pairs did not enter the nesting grounds until late May. In the southwest shore area the first pair to establish held a type A territory while later establishing pairs held type B territories. Differences in arrival times and territory type may be related to the age of the birds. Work with marked birds of known ages is needed to determine this.

Successful nest sites on Astotin Lake had three requirements: 1) easy access by water to the sites; 2) proximity to nest material; 3) protection from wave action. The sedge marshes offered numerous nest sites. The vegetation was of loose density offering easy access to the nest. The sedge hummocks provided nesting material and anchoring sites for the nests.

In areas offering numerous nesting sites, the territorial behaviour of the grebes delayed the nesting of some pairs, and may have prevented the nesting of other pairs. Agonistic interactions between pairs may have caused some egg loss during the incubation period, and desertion before all the eggs of the clutch hatched.

In 1969 the average clutch size for pairs on

Astotin Lake was 5.2 while the average brood size was 1.8. Known egg and chick losses did not account for this difference.

The territorial behaviour of the Red-necked Grebe seemed to be very flexible. When subjected to outside pressures the birds' territoriality seemed to grade into a dominance hierarchy system. How much of this was due to individual differences in pairs was not clear. Work with more pairs needs to be done.

The situation at Astotin Lake seemed to indicate that nest site availability was the prime factor controlling the spacing of pairs on the lake. The pairs were attracted to areas where there were potential nest sites. They then established themselves in the area by threatening and fighting with established pairs. How many pairs were unsuccessful at establishing was uncertain. Pairs that established later usurped parts of territories held by previously established pairs. The aggressiveness of the individual pairs determined the size of the territories. The aggressiveness of the pairs may have also determined whether they raised young successfully.

Agonistic behaviour either in the form of territoriality or dominance hierarchy may be a factor influencing the number of offspring produced by Red-necked Grebes. At low densities agonistic behaviour

may act as a spacing mechanism. At high densities this behaviour may continue to affect the spacing of pairs, but it may also affect the number of offspring produced by nesting pairs. Pairs nesting in high densities may spend more time threatening and fighting, thus delaying clutch initiation, and possibly increasing egg and chick loss through either accident or desertion. Subordinate pairs may produce fewer young than dominant pairs, but the general production of all pairs may be lower than if they were nesting at lower densities. This hypothesis needs to be tested.

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Appendix A. Some Invertebrate Fauna of Astotin Lake.

Ashelminthes	Rotifera	<i>Keratella</i> sp.
Annelida	Oligochaeta	<i>Chaetogaster lymnaei</i>
	Hirudinea	<i>Erpobdella punctata</i> <i>Macrobdella</i> sp. <i>Haemopsis</i> sp. <i>Nephalopsis obscura</i> <i>Glossiphonia complanata</i>
Mollusca	Basommatophora	<i>Lymnaea stagnalis</i> <i>Stagnicola palustris</i> <i>Helisoma trivolvis</i> <i>Physa gyrina</i> <i>Gyraulus paryus</i> <i>Aplexa hypnorum</i>
Chelicerata	Arachnida	<i>Hydracarina</i> spp.
Arthropoda	Crustacea	
	Amphipoda	<i>Gammarus lacustris</i>
	Cladocera	<i>Bosmina</i> sp. <i>Daphnia</i> sp. <i>Chydorus</i> sp. <i>Ceriodaphnia</i> sp.
	Copepoda	<i>Cyclops</i> sp. <i>Diaptomus</i> sp. <i>Paracyclops</i> sp.
	Ostracoda	1 species unidentified
	Insecta	
	Odonata	<i>Anax</i> sp. <i>Enallagma ebrium</i>
	Trichoptera	<i>Limnephilus infernalis</i> <i>Agrypnia</i> sp.
	Coleoptera	<i>Haliphus</i> sp. Dytiscidae 2 species
	Hemiptera	Corixidae 1 species
	Diptera	<i>Chironomus tentans</i> Ceratopogonidae 1 species

Appendix A. cont.

Ephemeroptera Baetidae 1 species

Compiled from Nursall (1968), Lin (1968) and results from analyzing the stomach contents of grebe chicks (see Appendix C.).

Appendix B. Birds nesting or seen with broods on Astotin
Lake in 1968 and 1969.

Podicipedidae

Red-necked Grebe
Pied-billed Grebe

Podiceps grisegena
Podilymbus podiceps

Ardeidae

Great Blue Heron
? Black-crowned Night Heron

Ardea herodias
Nycticorax nycticorax

Anatidae

Anserinae

Canada Goose

Branta canadensis

Anatinae

Mallard
Green-winged Teal
Blue-winged Teal
American Widgeon

Anas platyrhynchos
Anas carolinensis
Anas discors
Mareca americana

Aythya

Canvasback
Lesser Scaup
Common Goldeneye
Bufflehead

Aythya valisineria
Aythya affinis
Bucephala clangula
Bucephala albeola

Oxyurinae

Ruddy Duck

Oxyura jamaicensis

Rallidae

Sora Rail
American Coot

Porzana carolina
Fulica americana

Charadriidae

Killdeer

Charadrius vociferus

Scolopacidae

Wilson's Snipe
Lesser Yellowlegs
Spotted Sandpiper

Capella gallinago
Totanus flavipes
Actitis macularia

Laridae

Sterninae

Forster's Tern
Black Tern

Sterna forsteri
Chlidonias niger

Appendix B. cont.

Troglodytidae

Long-billed Marsh Wren

Telmatodytes palustris

Icteridae

Red-winged Blackbird

Common Grackle

Brown-headed Cowbird

*Agelaius phoeniceus**Quiscalus quiscula**Molothrus ater*

Appendix C. Food items found in the stomachs of eleven
Red-necked Grebe chicks found dead on
Astotin Lake in 1968 and 1969.

Annelida

Hirudinea (leeches)

Insecta

Odonata

Anisoptera

larval dragonflies

Zygoptera

Adult damselflies

Hemiptera

Corixidae (Water boatmen)

Coleoptera

Dytiscidae (predaceous diving beetles)

Larvae

Adults

Trichoptera

Phryganeidae

Agrypnia sp.

(larvae)

Chordata

Pisces

Gasterosteidae

Culaea inconstans

Feathers

Appendix D. Formulae used in calculating variance,
standard deviation, standard error, and
t test.

Where:

x = individual
samples

\bar{x} = mean

Σ = sum

N = number of
samples

s^2 = variance

s = standard deviation

SE = standard error

$$s^2 = \frac{x^2 - \frac{(\Sigma x)^2}{N}}{N-1}$$

$$s = \sqrt{s^2}$$

$$SE = \frac{s}{\sqrt{N}}$$

$$t = \frac{(\bar{x}_1 - \bar{x}_2) \sqrt{\frac{N_1 \times N_2}{N_1 + N_2}}}{\sqrt{\frac{s_1^2 (N_1 - 1) + s_2^2 (N_2 - 1)}{N_1 + N_2 - 2}}}$$

From: Simpson, George G. , Anne Roe, and Richard C.
Lewontin. 1960. Quantitative zoology.
Harcourt, Brace and Co. New York. 440 pp.

Appendix E. P values* of t indicating the significance of the differences between mean clutch sizes in different parts of Astotin Lake in 1969.

	Martin Bay	Creek Cove	South-west Shore	North-west Cove	Willow Clump	Cove north Long Island Point	Reed Island
Martin Bay		0.3	0.5	0.9	0.2	0.2	> 0.9
Creek Cove			0.5	0.3	> 0.9	> 0.9	0.3
Southwest Shore				0.9	0.3	0.4	0.7
Northwest Cove					0.2	0.3	0.9
Willow Clump						> 0.9	0.2
Cove north of Long Island Point							0.3
Reed Island							

* All values < unless indicated otherwise.

Appendix F. Means of measurements taken at the nest sites and at random points on Astotin Lake in 1969 and P values of t indicating the significance of the differences between these means.

Measurement and Location	\bar{x} at nest	\bar{x} at random points	P values *
Cove south of Long Island Point			
Distance from nest or random point to nearest sedge hummocks not touching nest or point	1.6 m	2.4	0.3
Basal area of the above sedge hummocks	0.16 m ²	0.22 m ²	0.5
Northwest Cove			
Distance from nest or point to nearest sedge hummocks not touching the nest or random point	1.7 m	1.8	0.9
Basal area of the above sedge hummocks	0.14 m ²	0.13 m ²	0.9

* All P values < unless indicated otherwise.

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